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VARIATION AND DISTRIBUTION OF THE PELAGIC AMPHIPOD CYPHOCARIS CHALLENGERI IN THE NORTHEAST PACIFIC (GAMMARIDEA: LYSIANASSIDAE)

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VARIATION AND DISTRIBUTION OF THE PELAGIC AMPHIPOD CYPHOCARIS CHALLENGERI IN THE NORTHEAST PACIFIC (GAMMARIDEA: LYSIANASSIDAE)

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The most common epipelagic gammaridean amphipod in Subarctic Water of the North Pacific is *Cyphocaris challengeri* Stebbing (1888, pp. 661–664, pl. 17). Other species of *Cyphocaris* occur in the North Pacific but are usually found at deeper levels than *C. challengeri*.

Altho the original description by Stebbing was detailed and well illustrated, it was based on a single juvenile specimen only about 5 mm long. The species was subsequently reported from the North and South Atlantic, the South Pacific, and the Indian Ocean but was not again recorded from the North Pacific until Thorsteinson (1941) reported its presence at Nanaimo, British Columbia. Its occurrence in the western North Pacific has been discussed recently by Birstein and Vinogradov (1955, 1958), who provided a map showing its worldwide distribution (1955, fig. 33).

In addition to recording the presence of *C. challengeri* at Nanaimo and giving some data on its variation with age, Thorsteinson described *C. kincaidi* from the Gulf of Alaska. Thorsteinson's new species was said to differ from *C. challengeri* in the more sharply produced pereonite 1, the more numerous setae on the gnathopods, the longer and narrower process of the basis of pereopod 5, and the longer telson.

It has been shown that certain characters of *C. challengeri* change with age: (1) In all species of *Cyphocaris* the head is directed down-

ward and partly covered above by the long pereonite 1, which is produced anteriorly into a process. The process varies in shape from low and bluntly rounded to long and sharply pointed. The process is most acute in young specimens and becomes more rounded as a *Cyphocaris* ages (Schellenberg, 1926b). (2) The number of teeth on the posterior margin of the basis of pereopod 5 decreases with age (Chevreux, 1916; Schellenberg, 1926a; Thorsteinson, 1941). (3) The length of the process of the basis of pereopod 5 increases in proportion to the rest of the limb (Thorsteinson, 1941). (4) The length of the telson increases relative to the length of uropod 3 (Schellenberg, 1926b).

In consideration of the variation with age detailed above, Shoemaker (1945) reduced *C. kincaidi* to a junior synonym of *C. challengeri*, an action accepted by subsequent authors (Birstein and Vinogradov, 1955, 1958, 1960; Gurjanova, 1962). In recent years, however, we have examined numerous samples collected with plankton nets and Isaacs-Kidd midwater trawls off the west coast of North America, containing larger numbers of *Cyphocaris* than had been available previously. The fact that almost all of the specimens could be assigned without difficulty to either *C. challengeri* or *C. kincaidi* as defined by Thorsteinson indicated the desirability of a reassessment of Shoemaker's decision to lump them, especially since in our collections the two forms were separated geographically as well as morphologically.

We wish to thank William Aron, then of the Department of Oceanography, University of Washington, for sending us representative samples of amphipods from M/V *Brown Bear* Cruises 199 and 202, and Bruce L. Wing, U.S. Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska, for midwater trawl collections from Lynn Canal, in the Alexander Archipelago, Southeast Alaska.

Distribution in the North Pacific

Since the form of the body of *C. challengeri* (sensu latu, including both *C. challengeri* and *C. kincaidi* sensu Thorsteinson) is correlated with its neritic-oceanic distribution, the neritic and oceanic distributions will be considered separately.

Oceanic distribution.—Figure 1 shows the offshore distribution of *C. challengeri*, based largely on Cruises 1, 5, and 9 of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) in 1949 and Cruises 199 and 202 of the University of Washington M/V *Brown Bear* in 1958. A few records from collections by the U.S. Bureau of Fisheries Steamer *Albatross* have been included.

Altho the CalCOFI cruises extended south about to the latitude of Punta Eugenia, Baja California, almost all the stations positive for

Cyphocaris occurred north of Cape Mendocino, Calif. (about 40.3°N). Likewise, *Brown Bear* Cruise 199 occupied stations south to about 32°N, or just south of the latitude of San Diego, but collected very few *Cyphocaris* south of 38°N, the approximate latitude of San Francisco.

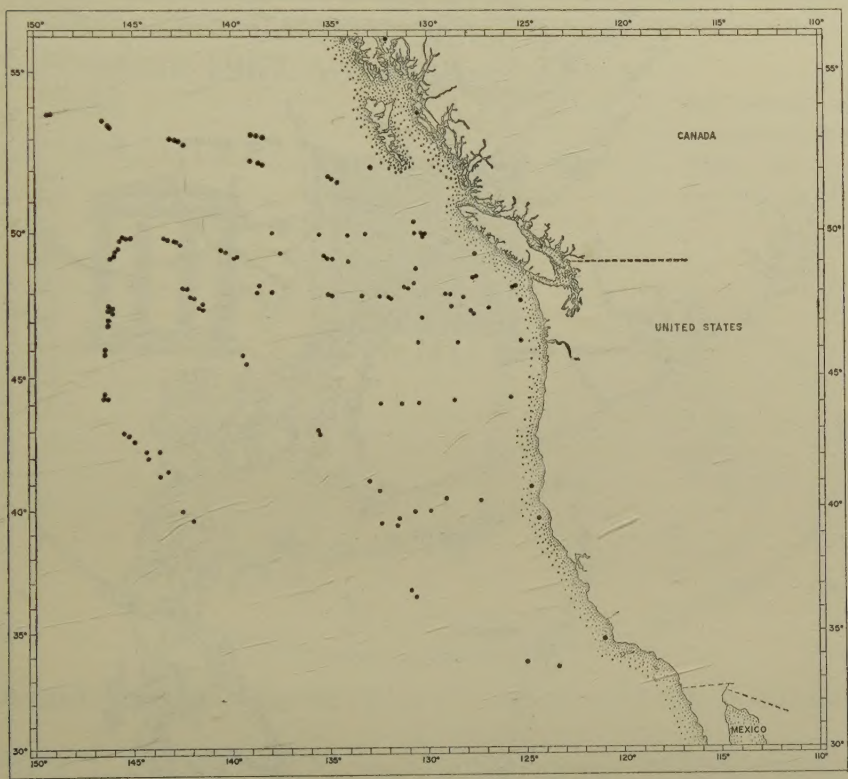

FIGURE 1.—Offshore distribution records of *Cyphocaris challengeri* in the northeastern Pacific.

The southern boundary of *C. challengeri* in the northeastern Pacific is comparable to that of other subarctic plankters: the euphausiids *Thysanoessa longipes* and *Tessarabrachion oculatus* (Brinton, 1962), and the chaetognath *Sagitta elegans* (Bieri, 1959). West of 150°W the southern boundary is not known, but presumably, as in other subarctic plankters, it runs parallel to and somewhat north of the North Pacific Drift. In the northwestern Pacific Bogorov (1958) lists *C. challengeri* as a characteristic species of the boreal plankton, the southern boundary of which approximates the convergence of the Oyashio and Kuroshio systems.

Little information is available on the depth distribution of *C. challengeri* in Subarctic Water. Birstein and Vinogradov (1955, fig. 32) show it ranging from near the surface down to 500–2000 m and possibly deeper. Bogorov (1958) refers to it as a surface zone (0–200 m) species. In CalCOFI Cruises 5 and 9, which sampled the upper

FIGURE 2.—Distribution records of *Cyphocaris challengeri* in the Puget Sound region.

70 m with 1-m plankton nets, *C. challengeri* was taken mainly at night. Five of the six positive stations of Cruise 5 (July 1949) were night stations; an average number of 16/1000 m^3 was taken at the night stations, and 1/1000 m^3 at the day station. Of the 13 positive stations on Cruise 9 (November 1949), 12, with an average catch of 12/1000 m^3, were night stations, whereas only 1/1000 m^3 was caught at the day station. There is clearly an upward movement of the population at night.

NERITIC DISTRIBUTION.—As shown in figure 2, *C. challengeri* is widespread in the Puget Sound region. To the north it also occurs in Hecate Strait and in at least some of the straits between the islands of the Alexander Archipelago. Details of its vertical distribution are poorly known, but large numbers were taken with Isaacs-Kidd trawls in the upper 100 m in Lynn Canal, Alexander Archipelago.

Global Distribution

The world-wide distributional pattern of *C. challengeri* outside of the North Pacific, shown in figure 3, is puzzling. Many zooplankton species inhabiting Subarctic Water do not occur elsewhere, for example: the polychaete worm *Tomopteris pacificus* (Tebble, 1962); the

FIGURE 3.—World distribution records of *Cyphocaris challengeri* outside of the North Pacific.

copepods *Calanus cristatus*, *C. plumchrus*, *Eucalanus bungii bungii*, *Candacia columbiae*, and others (Brodsky, 1957; Johnson, 1941; Omari, 1965); the euphausiids *Euphausia pacifica*, *Tessarabrachion oculatus*, and *Thysanoessa longipes* (Brinton, 1962); and the hyperiid amplipod *Parathemisto pacifica* (Bowman, 1960). As far as we know, none of the subarctic epipelagic plankters has a global distribution comparable to that of *C. challengeri*. It is perhaps significant that almost all the collections outside of the North Pacific were made with nets that had been lowered to considerable depths, mainly 1000–3000 m. Altho these were not closing nets and the depth of capture is uncertain, it is possible that *C. challengeri* undergoes a submergence at lower latitudes. An alternative possibility, that more than one species is involved, cannot be properly evaluated until abundant material from all parts of the geographic range becomes available.

Morphological Variation

SHAPE OF PEREONITE 1.—All of the oceanic specimens had the more sharply produced pereonite 1 described by Thorsteinson for *C. kincaidi*. In profile it is very sharp and high in small specimens

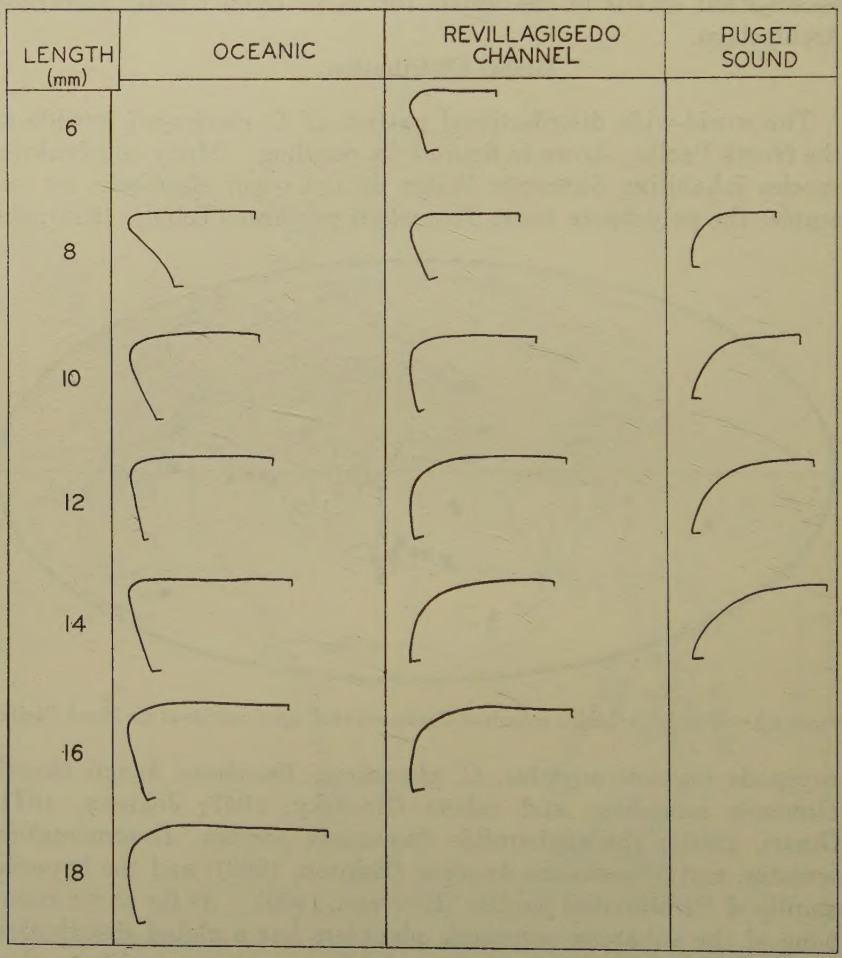

FIGURE 4.—Profiles of pereonite 1 of three populations of *Cyphocaris challengeri*, showing variation with age.

and as the animal grows the process becomes more rounded and lower. A series of profiles of pereonite 1 from representative growth stages is shown in figure 4. In a similar series from inshore populations collected in the Puget Sound region, pereonite 1 is also more produced in small specimens, but it does not approach the condition in oceanic specimens. Specimens from Lynn Canal and Revillagigedo

Channel, Alexander Archipelago, are intermediate, but appear to show more resemblance to the Puget Sound than to the oceanic specimens.

In order to express quantitatively the shape of pereonite 1, a simple index has been devised. The straight-line distance between

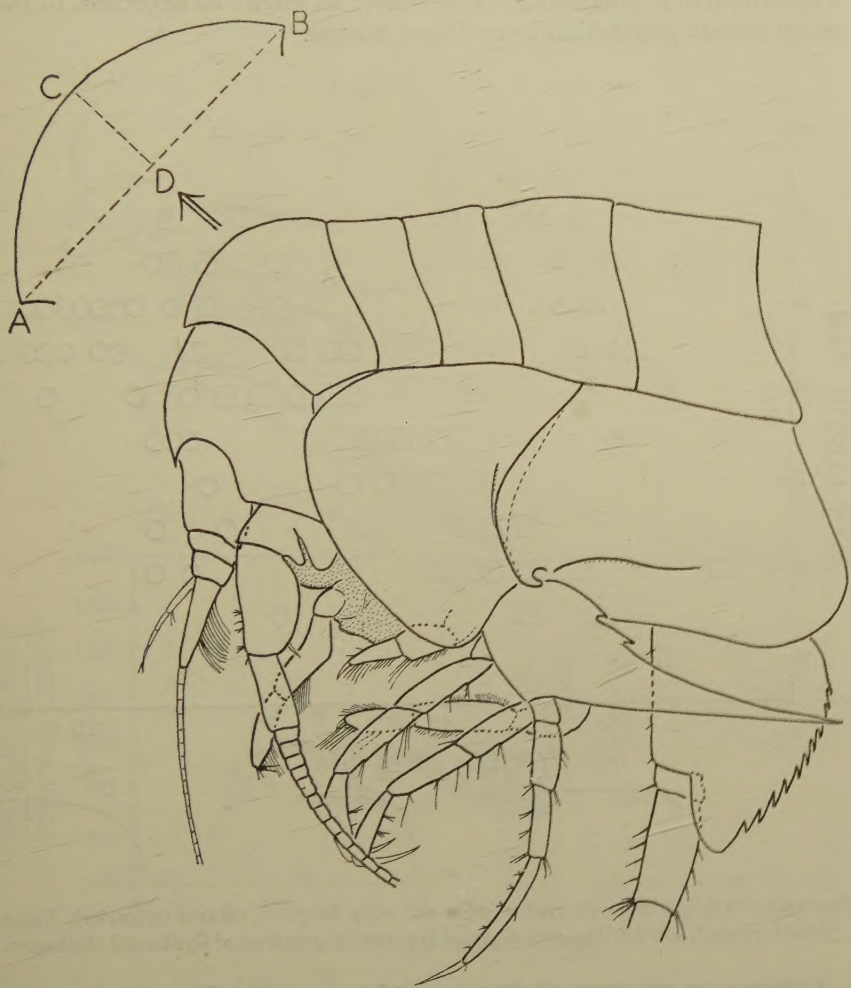

FIGURE 5.—Anterior end of *Cyphocaris challengeri*, lateral $\left(\frac{CD}{AB} \times 100 = \text{cyphos index}\right)$.

the anterodorsal and posterodorsal margins, viewed laterally, is divided into the longest perpendicular from this line to the dorsal margin (fig. 5). The quotient is multiplied by 100 to give an index which may be termed the "cyphos index" (from κυφος="hump," the first part of the generic name *Cyphocaris*="hump-head"). In figure 6, cyphos indices are plotted against body length for the oceanic

form and for neritic populations from Puget Sound and Alexander Archipelago. The change with age to a flatter pereonite 1 is evident; the figure also demonstrates that in this character the Alexander Archipelago population is intermediate between the oceanic and Puget Sound populations, but is closer, as might be expected, to the other neritic population from Puget Sound.

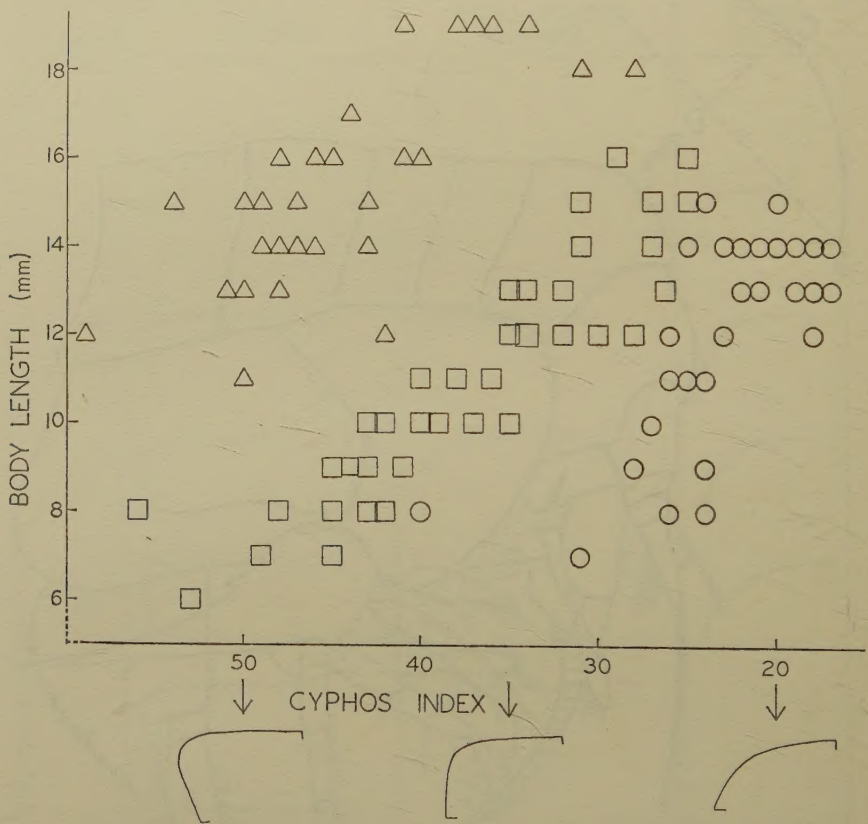

FIGURE 6.—Relation between cyphos index and body length in oceanic (triangles), Puget Sound (circles), and Revillagigedo Channel (squares) populations of *Cyphocaris challengeri*.

LENGTH OF PROCESS OF PEREOPOD 5 BASIS.—In figure 7 the ratio of the length of the process of the basis to the length of the distal segments of the limb is plotted against body length. The ratio is clearly higher in the oceanic form and does not appear to vary with age. In figure 8 the ratios obtained for the three populations, lumping all growth stages, are represented according to the graphical method of Hubbs and Hubbs (1953). The wide separation of the oceanic from the two neritic populations is evident. The difference between the means of the latter populations is statistically significant

(t=2.6) but small compared to their divergence from the oceanic population. Note that in this character the Puget Sound population is intermediate, whereas the Revillagigedo Channel population was intermediate with respect to the cyphos index.

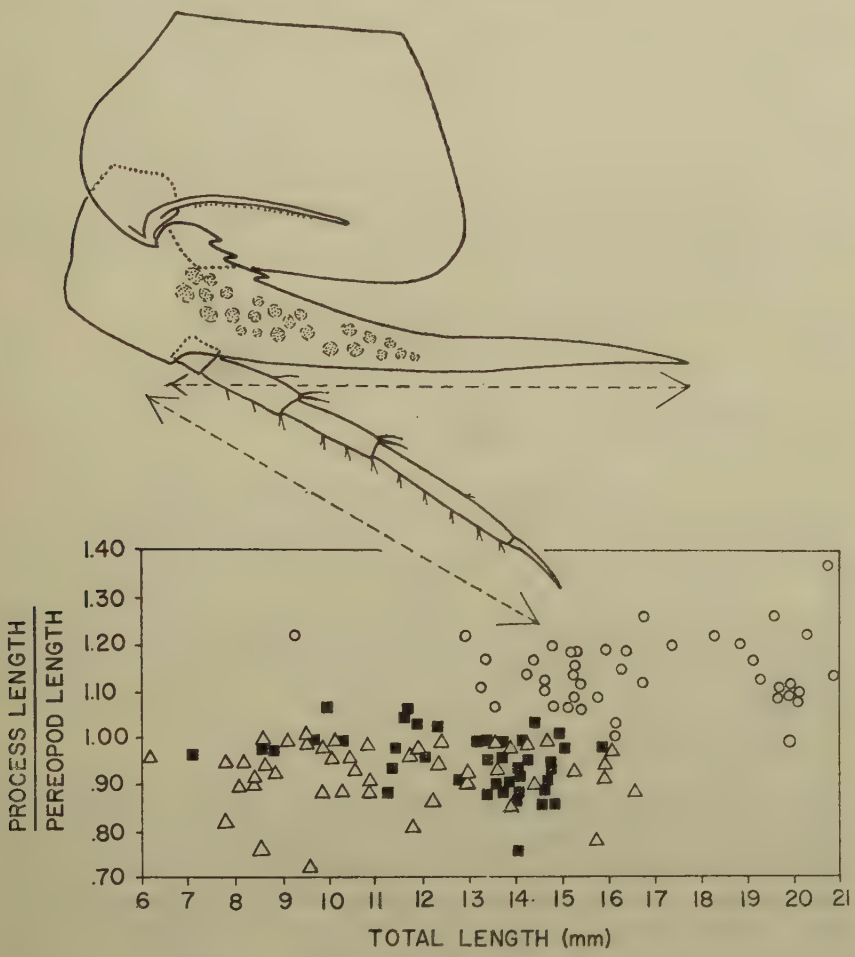

FIGURE 7.—Ratio of length of basal process to that of distal segments in pereopod 5 plotted against body length in oceanic (circles), Puget Sound (solid squares), and Revillagigedo Channel (triangles) populations of *Cyphocaris challengeri.*

RATIO OF LENGTH OF 3RD UROPOD TO LENGTH OF TELSON.—In figure 9 the ratio of the length of uropod 3 to that of the telson is plotted against body length. Altho there is considerable variation, it can be seen that the ratio decreases from 1.4–1.8 in juveniles to 1.0–1.2 in adults. The rate at which the ratio decreases is approximately equal in all three populations, but for a particular body length the

ratio tends to be lower in the Puget Sound population, the adults of which are smaller than those of the other two populations.

Origin of Variation in *Cyphocaris challengeri*

Movement of Subarctic Water is from west to east, via the Subarctic or Aleutian Current (Sverdrup, Johnson, and Fleming, 1942). As this current approaches the American coast, it divides into the Alaska Current, which moves north into the Gulf of Alaska, and the California Current, which flows south along the coast of California. From the direction of the currents it is assumed that the coastal population of *C. challengeri* has been derived from the oceanic population. Any large contribution of individuals to the oceanic population

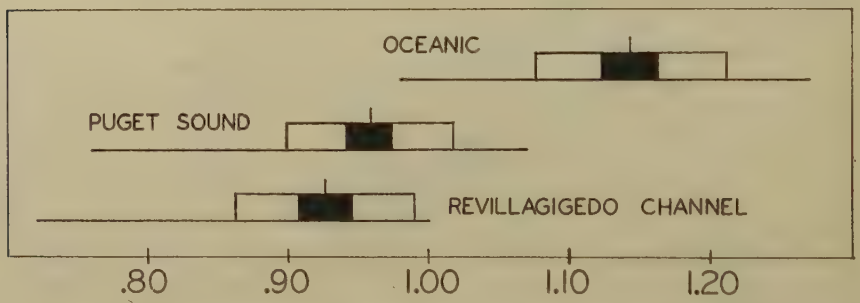

FIGURE 8.—Ratio of length of basal process to that of distal segments of pereopod 5 for three populations of *Cyphocaris challengeri* (for each diagram the horizontal line represents the sample range, the vertical line the sample mean, and the black rectangle the value of 2 standard errors on each side of the mean; the distance from a mean to the edge of a white rectangle equals the value of 1 standard deviation).

from the coastal population is precluded by the circulation in the coastal inlets. The inlets are deep estuaries, with a surface layer of low salinity water formed by river runoff overlying a deep layer of denser high salinity water. The surface water flows seaward and deep water enters the inlets from the ocean. (Waldichuk, 1957; Herlinveaux and Tully, 1961; Pickard, 1961). The effects of tides and other factors complicate the picture, but if it is assumed that *Cyphocaris* avoids the low salinity surface layer, the circulation would tend to hinder its seaward movement. Hence, any genetic changes that might accumulate in the coastal populations would not affect the oceanic population.

The origin of the coastal forms can be explained by the mechanism proposed by Buzzati-Traverso (1958) and used by McGowan (1963) to explain the distribution of two forms of the pteropod *Limacina helicina* in the subarctic North Pacific.

When the inlets were first invaded by *Cyphocaris*, only those individuals genetically pre-equipped to endure the unaccustomed coastal conditions were able to survive and breed successfully. As the coastal populations multiplied in the new environment, selection and adaptation proceeded until the morphologically distinct coastal forms evolved. Altho immigrants continued to arrive from the

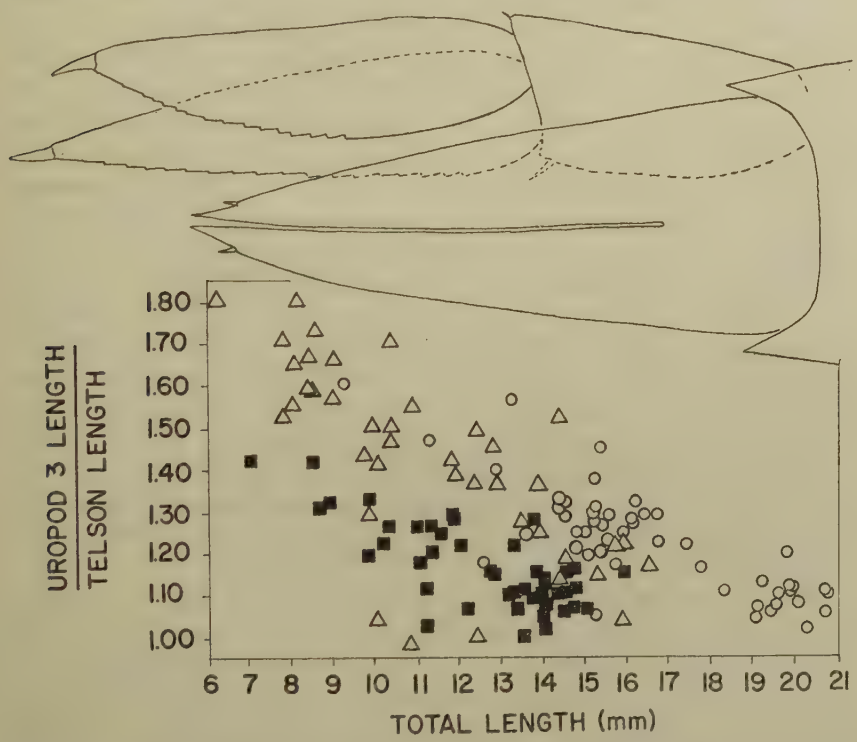

FIGURE 9.—Ratio of length of uropod 3 to that of telson plotted against body length for oceanic (circles), Puget Sound (solid squares), and Revillagigedo Channel (triangles) populations of *Cyphocaris challengeri*.

the oceanic population, most of them could not compete successfully under coastal conditions. Populations in Puget Sound and the inlets of the Alexander Archipelago evolved independently and now have demonstrable morphological differences. It is possible that other coastal populations, now unstudied, will also show recognizable differences.

From the foregoing analysis it is clear that the northeast Pacific population of *Cyphocaris challengeri* includes an oceanic form in Subarctic Water and inshore forms inhabiting coastal waters of western North America from Puget Sound northward. The oceanic

form, considered a new species, *C. kincaidi*, by Thorsteinson, is distinguished by its larger size, more produced pereonite 1 (higher cyphos index) and a longer process on pereopod 3 than populations from Revillagigedo Channel and Lynn Canal, Alexander Archipelago. The two inshore forms are morphologically more similar to each other than to the oceanic form.

We are now faced with the problem of whether Thorsteinson's *C. kincaidi* should be reestablished as a species distinct from *C. challengeri*. First, however, we must consider to which form Stebbing's *C. challengeri* belongs. Unfortunately, Stebbing's single type specimen was so immature (about 5 mm) that morphological characters cannot be relied upon. Concerning the type-locality Stebbing states: "The label on the mounted specimen states that it was taken 400 miles north of the Sandwich [=Hawaiian] Islands; probably near station 256." Murray (1895) lists it as a constituent of the surface plankton of Station 256, located at 30°22′N, 154°56′W. At our request Mr. E. C. Jones, Bureau of Commercial Fisheries Biological Laboratory, Honolulu, examined a number of plankton samples collected near the type-locality, but none of these samples contained *Cyphocaris*. Mr. Jones agrees with us that *C. challengeri* is a subarctic species and would not be expected to occur in Central Water. It is not unreasonable to suspect that the type specimens of *C, challengeri* may have been collected farther north than Station 256. perhaps during the traverse of H.M.S. *Challenger* across the North Pacific from Japan.

Despite the uncertainty of the exact position of the type-locality, it must be presumed that *C. challengeri* is the oceanic form, with the more produced pereonite 1. But, as we have seen, Thorsteinson described the oceanic form as a new species, *C. kincaidi*, and assigned the Puget Sound form to *C. challengeri*. Hence, *C. kincaidi* is a junior synonym of *C. challengeri*, and, if the inshore form (*C. challengeri* sensu Thorsteinson) should be considered to be specifically or subspecifically distinct, a new name would be required.

Because the differences between the oceanic and coastal forms are much less than those separating the known species of *Cyphocaris* from one another and because these differences vary from one coastal population to another, we have chosen not to consider the two forms as distinct species. For the present it seems most convenient to refer to "oceanic" and "coastal" forms and to further designate the coastal form populations by locality.

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